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WESTERN GUATEMALA A SECONDARY CENTER OF ORIGIN OF CULTIVATED MAIZE VARIETIES¹

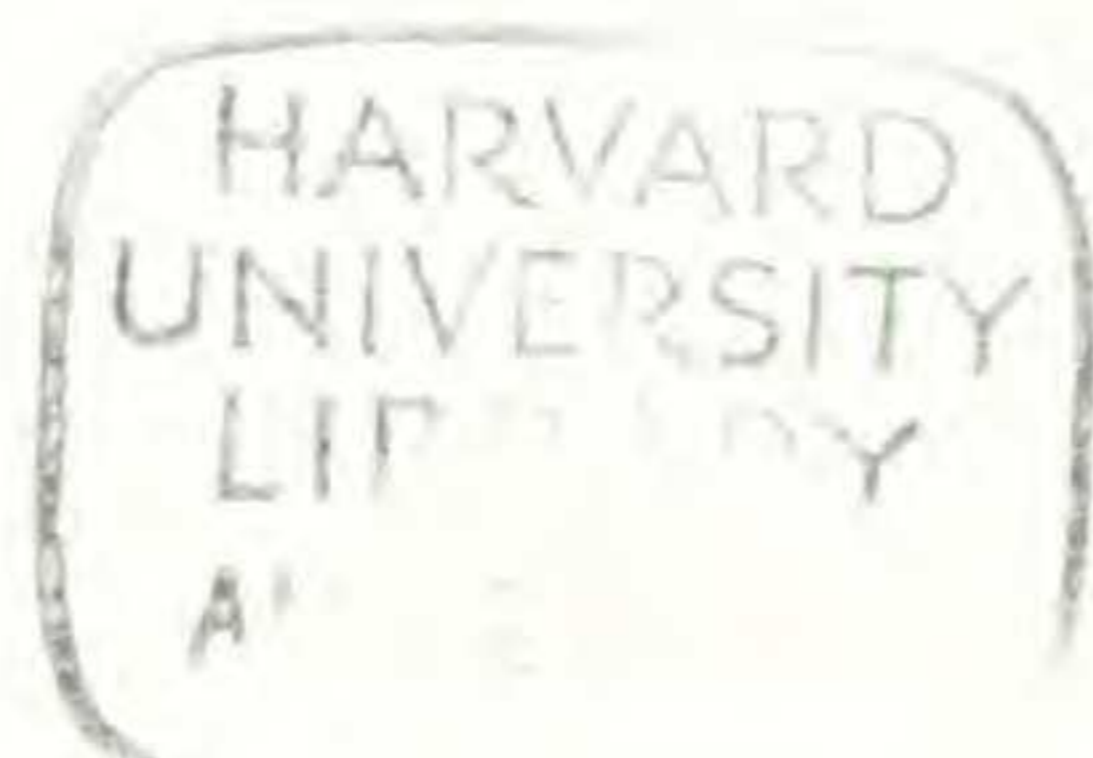
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IN A PREVIOUS PUBLICATION Mangelsdorf and Reeves (18) advanced the tripartite hypothesis: 1. that cultivated maize originated from a wild form of pod corn which was once, and perhaps still is, indigenous to the lowlands of South America; 2. that *Euchlaena* (teosinte), the closest relative of maize, is a recent product of the natural hybridization of *Zea* and *Tripsacum* which occurred after cultivated maize had been introduced by man into Central America; 3. that new types of maize originating directly or indirectly from this cross and exhibiting admixture with *Tripsacum* comprise the majority of Central and North American varieties.

The three parts of this hypothesis, although presenting an integrated picture of the origin of maize, are nonetheless to some extent independent of each other. The actual discovery of wild pod maize, for example, while completely establishing the first postulate, would do no more than lend strong indirect support to the second and third. Overwhelming evidence that teosinte is a hybrid of maize and *Tripsacum* would not prove that the majority

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of Central and North American varieties are contaminated with *Tripsacum*. It becomes necessary therefore to attack separately the numerous problems which are suggested by each of the three more or less independent parts of the hypothesis. This paper concerns itself only with the third. How extensive has been the introgression of *Tripsacum* into maize to produce new types and where is the region—the secondary center of origin of cultivated maize varieties—in which this phenomenon has occurred?

In approaching this problem the conclusions of Mangelsdorf and Reeves are utilized as the working hypothesis and the results obtained are discussed in terms of that hypothesis. Other interpretations can be made, however, and are discussed later.

In the previous publication it was pointed out that in the number and position of chromosome knobs, teosinte, as it is in many other characteristics, is intermediate between North American maize and *Tripsacum*.² This fact suggested that pure maize, uncontaminated by *Tripsacum*, might possess knobless chromosomes. Such varieties were sought and found in the Andean region of Peru, Bolivia and Ecuador. It was also found that these varieties differ from the majority of those of North and Central America in lacking characteristics which might have been derived from *Tripsacum*. The Andean varieties are, to use a term proposed by Anderson and Erickson (1), much less “*Tripsacoid*” than the predominating maize of Central or North America.

Another corollary of this same line of reasoning is

²Chromosome knobs are deeply-staining pycnotic enlargements visible at high magnifications when the chromosomes are in the pachytene stage. They have been observed only in the three American Maydeae: *Tripsacum*, *Euchlaena* and *Zea*. In *Tripsacum* and Guatemalan teosinte they are numerous and are confined to the ends of the chromosomes. In maize and Mexican teosintes their number is variable and their position frequently subterminal.

that we should expect to find the most *Tripsacoid* maize, maize with the largest number of chromosome knobs, in the general region where teosinte occurs most abundantly as a plant growing in the wild, the region where it presumably originated from the hybridization of maize and *Tripsacum*. We might, however, also have a reasonable expectation of finding in this same general region non-*Tripsacoid* varieties, descendants of the pure maize which had been introduced from South America and which had been the only type grown before the hybridization with *Tripsacum* occurred.

Since western Guatemala is the only region so far discovered where teosinte grows in profusion in a wild state, since it is a region where *Tripsacum* is common, and finally since it is a region of numerous mountains and valleys—natural barriers which would enable varieties once established to maintain themselves indefinitely in a relative state of genic stability—it appeared to be the most promising region for beginning an investigation of this problem.

At our instigation Dr. F. W. McBryde, Department of Geography, Ohio State University, who spent more than a year in Guatemala and southern Mexico as National Research Council Fellow, has made comprehensive collections of maize varieties in these regions. His collection from western Guatemala was especially complete including 318 ears from thirty-eight localities in thirteen Departments. We are also indebted to Dr. McBryde for various data on the corn varieties and the localities where they were collected.

Even a cursory study of this collection demonstrates at once the great diversity of maize in western Guatemala. Here, in an area less than half the size of the state of Iowa, are found probably more distinct types of corn than occur in the entire United States.

Plants from 200 ears of this collection were grown in duplicate plantings at New Haven, Connecticut,³ and Forest Hills, Massachusetts, in the summer of 1941. The remaining 118 ears were omitted partly because of limitations of time and space but mainly because they appeared to be duplicates or near-duplicates of those selected for planting from the same locality. The great majority of the varieties were tall-growing, vigorous and late in maturity. In spite of an unusually favorable season and absence of early frost, not all varieties reached a stage where material for cytological studies could be collected and only 162 were examined cytologically. To this extent our sampling of Guatemalan maize is not completely random because the more Tripsacoid varieties, those with largest numbers of chromosome knobs, are among the later maturing ones.

Again, because of the limitations of time, knob number was determined on only one plant in each variety. This admittedly is not an adequate sample for establishing the average knob number of a variety. The primary goal in this case, however, was to sample the region rather than the variety. In considering relationships, discussed later, between knob numbers and other characteristics, it should be borne in mind that significant relationship can be shown in spite of rather than because of inadequate sampling of varieties. Had the average knob numbers for each variety been more precisely determined, even more significant relationship could probably have been shown.

No attempt was made to identify each chromosome on which a knob was borne nor to determine the position of each knob but in examining the preparations all of the eighteen knob positions which Longley (14) has described

³ We are indebted to Dr. D. F. Jones and other members of the staff of the Connecticut Agricultural Experiment Station for invaluable assistance in connection with the studies made at New Haven.

TABLE I

Knob numbers of maize varieties from Guatemala

Department	Locality	Number of Varieties	Range of Knob Nos.	Average Knob No.
Quezaltenango	Almolonga	3	4-6	4.7
"	Cantel	5	4-6	4.8
"	San Juan Ostuncalco	17	3-8	4.9
"	San Martin Sacatepequez	5	4-6	5.6
"	Olintepeque	12	3-9	6.2
"	Quezaltenango	2	6-8	7.0
	Total and Average	44	3-9	5.4
Totonicapan	San Francisco el Alto	4	4-6	5.2
"	San Cristóbal Totonicapan	4	3-10	5.5
"	Momostenango	3	9-12	10.7
	Total and Average	11	3-12	6.8
El Quiche	Santo Tomás Chichicastenango	9	5-9	7.0
"	San Pedro Jocopilas	11	3-12	7.9
	Total and Average	20	3-12	7.5
Huehuetenango	Santa Eulalia	4	1-6	4.0
"	San Juan Atitan	4	1-9	4.8
"	San Juan Ixcoy	6	3-8	5.2
"	San Sebastián Coatán	6	1-11	6.0
"	San Martin Cuchumatán	4	4-11	8.5
"	Huehuetenango	6	6-14	8.7
"	Todos Santos Cuchumatán	2	4-14	9.0
"	Chalchitan	5	5-11	9.8
"	San Miguel Acatan	1	11	11.0
"	Jacaltenango	2	11-12	11.5
"	San Antonio Huista	7	9-14	12.4
"	Santiago Petatán	1	14	14.0
	Total and Average	48	1-14	8.1
Chimaltenango	Tecpam	4	7-11	9.5
Baja Verapaz	Rabinal	7	6-12	9.6
Suchitepequez	Chicacao	1	10	10.0
Solola	San Lucas Tolimán	1	9	9.0
"	Santa Catarina Palopó	1	10	10.0
"	Panajachel	4	8-13	10.8
	Total and Average	6	8-13	10.4
Jalapa	San Pedro Pinula	4	7-10	8.2
"	San Luis Jilotepeque	2	12-16	14.0
"	Cruz de Villeda	1	15	15.0
	Total and Average	7	7-16	10.8
Guatemala	Chinautla	1	11	11.0
Retalhuleu	San Sebastián Retalhuleu	4	11-14	12.2
Escuintla	Puerto San José	3	11-14	12.3
"	San Lucia Cotzumalguapa	3	10-15	12.3
	Total and Average	6	10-15	12.3
Chiquimula	Quezaltepeque	1	12	12.0
"	Camotán	2	13-16	14.5
	Total and Average	3	12-16	13.7
	Grand Total and Average	162	1-16	7.9

in maize were encountered at least once. In addition three positions not previously reported, two on the long arm of the tenth and another terminating the short arm of the first chromosome, were seen bearing enough pycnotic material to require their being classed as knobs.

Table I shows the departments and localities from which the varieties were collected; the range in knob numbers and average knob numbers. The thirty-eight localities and their average knob numbers are also shown in the accompanying map.

The average knob number for the 162 varieties is 7.9, the highest average number so far reported for any country or region studied. Even without further analysis this bears out the assumption that the highest knob numbers should occur in the general region where teosinte is most abundant in the wild state.

The second and somewhat contradictory assumption that varieties with knobless chromosomes might also be encountered in this same general region has not been completely met, although it has been closely approached. Three varieties were found with only one knob and it is reasonable to suppose that knobless plants would have been discovered in these or other varieties had additional studies been possible. Indeed Dr. R. G. Reeves, working with other samples from Guatemala, has found one variety segregating for knobless plants.

Of particular interest is the knob situation in the Department of Huehuetenango. In a small area of less than two hundred square miles, approximately the area bounded by a polygon in which the points are formed by the localities of San Antonio Huista, Santiago Petatán, San Martin Cuchumatán, Todos Santos Cuchumatán, San Juan Ixcay, Santa Eulalia, San Sebastian Coatán, San Miguel Acatan and Jacaltenango, are found knob numbers ranging from one to fourteen. Here in an area scarce-

ly larger than that of New York City are found almost all the knob positions known in maize from any part of the world. Here too are the localities where Kempton and Popenoe (9) found teosinte occurring as the dominant species over thousands of acres,⁴ the only place so far discovered where this condition exists, and where they also found a species of *Tripsacum* growing in great profusion. Here then are all the elements to make the picture complete: Andean types of corn almost completely lacking in chromosome knobs, slightly contaminated descendants of the pure corn introduced from South America; *Tripsacum* growing in profusion on the hillsides and furnishing the opportunity for natural hybridization; the most *Tripsacoid* type of *Euchlaena* known, presumably the primary product of the hybridization of *Zea* and *Tripsacum*, occupying thousands of acres as the dominant species, and finally *Tripsacoid* maize varieties, secondary products of the hybridization, showing all degrees of admixture with *Tripsacum*.

Here then, if diversity is any criterion whatever, is certainly a well-defined center of origin of cultivated maize. According to the hypothesis of Mangelsdorf and Reeves this is the secondary center of origin, the place where new types have come into existence as the result of hybridization of maize and *Tripsacum*. According to older hypotheses which have maize deriving directly from teosinte, or all three of the American *Maydeae*, maize, teosinte and *Tripsacum* deriving from a common ancestor, this is the primary center of origin of cultivated maize. In any event it is obviously a concentrated center of diversity not only in the external morphological characteristics of the ears

⁴ Teosinte in this area is even more common than the observations of Kempton and Popenoe indicate, since McBryde has found it growing in great abundance between Santiago Petatán and Santa Ana Huista, a locality about four miles west of San Antonio Huista.

but also in certain internal morphological features of the chromosomes.

Varieties with still higher knob numbers, numbers up to sixteen, were found in other parts of Guatemala. No particular significance attaches to this, however, for the sampling errors are large and it is reasonable to assume that plants with as many as sixteen or more knobs would be discovered in this area if an exhaustive search were made. This is especially probable since some of the most Tripsacoid varieties from this area, being very late in maturity, were not examined cytologically. Of the twenty-one varieties planted from the four localities in Huehuetenango with highest knob numbers, only eleven were early enough for cytological examination.

Knob number is only one of the characteristics by which the degree of contamination with *Tripsacum* can be measured. It is perhaps one of the most useful because it is a precise quantitative datum. We assume that the chromosome knobs of present-day corn were derived from *Tripsacum* through teosinte and on that assumption the number of knobs becomes a rough measure of the amount of *Tripsacum* admixture. It is desirable, however, to test this assumption by determining whether knob number is associated with other characteristics which might have been derived from *Tripsacum*.

That there is such a relationship can be immediately discerned even without studying other characteristics in detail. When ears of these varieties were received from Dr. McBryde it was at once apparent that some of them resembled quite closely certain varieties from the Andean region. These were tentatively designated as "Andean" types. The average knob number of this group, comprising sixteen varieties, is 4.7, only slightly more than half the average number 7.9 for the population as a whole. In other words it was possible on the basis of the general

appearance of the ears alone to sort out varieties which later proved to have low knob numbers.

More detailed studies, the results of which are set forth in Table II, show that knob number is associated with many other characteristics. Before considering these relationships it should be explained how they are determined. Since the data are not extensive in a statistical sense and in some cases represent qualitative rather than quantitative scoring, elaborate statistical treatment is not indicated and in some instances not feasible. P values, which are a measure of significance, were derived from Chi square values, computed from fourfold tables in which the population was arbitrarily divided into two groups on the basis of knob numbers and into two additional groups on the basis of the other character under consideration. In several cases where additional refinement seemed desirable the second division involved three categories instead of two.

In quantitative characters other than knobs, separation was made at the mean and the two groups were approximately of equal size. In the case of knob numbers, however, it was found by examination of the data and preliminary computations that a more natural grouping could be made if varieties with six knobs or less were included in the low-knob group, varieties with seven knobs or more in the high-knob group. P values are only slightly higher however, and in several instances lower, if the separation is made at the mean.

RELATIONSHIPS BETWEEN KNOB NUMBERS AND OTHER CHARACTERISTICS

Altitude

Adaptation to altitude may well be one of the characteristics involved in the introgression of *Tripsacum* into maize. At any rate there is an obvious relationship be-

TABLE II. The relationship between knob number and other characters in maize from Guatemala

No. Knobs.....	1	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Weighted Averages		x ²	P
																Low	High		
No. Varieties*.....	3	10	18	14	23	16	10	13	7	19	14	4	7	2	2				
Av. Altitude where collected (ft.).....	7928	7954	7836	7672	7557	6458	7216	6622	5973	4904	3877	4920	4169	2050	2460	7729	5417	43.37	<.01
Av. Length of Ear (cm.).....	16.7	14.8	17.2	16.9	17.2	17.6	17.9	19.1	20.1	19.4	16.2	18.2	18.3	18.5	11.5	16.8	18.1	2.15	>.05
Av. Diameter, Base of Ear (mm.).....	56.7	48.8	51.8	50.0	50.0	47.7	50.0	48.8	52.1	48.4	47.9	50.0	49.3	47.5	40.0	50.6	48.7	0.24	>.05
Av. Diameter, Tip of Ear (mm.).....	28.3	30.6	30.6	31.4	32.3	32.7	33.0	31.9	35.0	32.1	36.8	35.0	35.0	37.5	32.5	31.3	33.7	4.88	.04
Tip/Base Index.....	49.9	62.7	59.1	62.8	64.6	68.6	66.0	65.4	67.2	66.3	76.8	70.0	71.0	78.9	81.2	61.8	69.3	8.59	<.01
Tapering Index.....	2.99	2.52	2.38	2.20	2.06	1.78	1.90	1.81	1.63	1.74	1.43	1.65	1.58	1.14	1.63	2.28	1.69	14.96	<.01
Av. No. Rows of Grain.....	16.7	13.8	11.4	11.9	12.5	12.7	12.2	12.6	14.6	12.5	12.9	13.5	13.4	13.0	13.0	12.4	12.9	1.17	>.05
Ratio of Irregular to Distinct Rows.....	3:0	10:0	16:2	10:4	14:9	6:10	3:7	1:12	1:6	4:15	3:11	0:4	2:5	0:2	0:2	53:15	20:74	51.38	<.01
Ratio of Yielding to Firm Cobs.....	3:0	6:4	11:7	8:6	13:10	5:11	5:5	8:5	3:4	8:11	7:7	2:2	3:4	1:1	2:0	41:27	44:50	2.86	>.05
Av. No. Seeds per Row.....	24.7	27.3	29.2	28.5	29.7	32.3	34.5	33.0	38.3	37.5	38.1	35.0	35.4	43.0	28.5	28.8	35.5	21.83	<.01
Av. No. Seeds per Cm.....	1.48	1.84	1.70	1.68	1.73	1.83	1.93	1.73	1.90	1.94	2.35	1.92	1.94	2.32	2.48	1.72	1.97	8.59	<.01
Av. Wt. of 10 Seeds (gms.).....	4.5	3.8	4.8	4.6	4.0	3.7	3.7	3.8	3.3	3.4	3.0	3.4	3.0	3.0	2.0	4.3	3.4	16.40	<.01
Ratio of Flint and Flour to Dent Grains.....	3:0	7:3	14:4	12:2	15:8	13:3	8:2	10:3	3:4	9:10	3:11	1:3	2:5	0:2	0:2	51:17	49:45	8.95	<.01
Ratio of Presence to Absence of Endosperm Color	3:0	8:2	11:7	10:4	14:9	7:9	2:8	8:5	2:5	12:7	5:9	4:0	2:5	0:2	0:2	46:22	42:52	8.46	<.01
Ratio of Presence to Absence of Purple Plant Color	0:3	0:10	0:18	0:14	1:22	1:15	0:10	0:13	2:5	3:16	2:12	1:3	2:5	1:1	0:2	1:67	12:32	6.94	<.01
Ratio of Coarse and Intermediate to Fibrous Roots	3:0	10:0	18:0	11:3	21:2	11:5	7:3	13:0	6:1	14:5	5:9	1:3	0:6	1:1	0:2	63:5	58:35	19.31	<.01
Ratio of Strong to Medium and Zero Pubescence..	2:1	10:0	14:4	10:4	19:4	11:5	7:3	4:9	2:5	4:15	1:13	0:4	0:7	0:2	0:2	55:13	29:65	39.39	<.01
Av. Percentage of Smutted Plants.....	71.9	53.6	52.1	52.3	58.4	33.9	30.0	42.4	22.4	33.1	38.0	44.0	30.3	48.8	65.0	55.4	35.4	8.78	<.01
Av. Percentage of Lodged Plants.....	67.4	78.3	67.5	66.4	70.3	44.2	52.6	49.1	36.6	41.3	28.5	16.9	26.3	23.8	5.0	69.8	38.5	32.85	<.01

* Five varieties with branched ears omitted in measurements on ear diameters and tapering.

tween altitude and knob number. Precise data on altitudes of the thirty-eight localities included in this study are not available but approximate altitudes were determined from a topographical map prepared by Dr. McBryde from original surveys and other sources. In spite of the lack of precise data there is a highly significant relationship (P is less than .01) between number of knobs and altitude of the locality from which the maize was collected. Maize with one or three knobs was collected at altitudes averaging approximately 8000 feet. Maize with fifteen or sixteen knobs was collected at altitudes averaging 2000–2500 feet. Intervening values show approximately a linear relationship.

We interpret this relationship to mean that the non-Tripsacoid or Andean type of maize introduced from South America was then, as it is now, poorly adapted to culture at low altitudes. If it was grown at all at low altitudes, it was immediately replaced by Tripsacoid maize as soon as the latter had come into existence. At high altitudes, however, the pure maize has been able to hold its own. A similar situation has already been reported for South America where knobless types predominate in the Andean regions of Peru, Bolivia and Ecuador, while Tripsacoid types with knobby chromosomes are most frequent in the lowlands. There is some indication that Tripsacoid maize can succeed and is to some extent replacing non-Tripsacoid maize even at high altitudes. Of the sixty-eight varieties with six knobs or less, only two are found at an altitude lower than 6500 feet; while varieties with twelve knobs or more are frequently encountered at approximately 5000 feet and occasionally at 6500 feet and higher.

The fact that non-Tripsacoid varieties of maize are found only at high altitudes in Guatemala is not necessarily in conflict with the assumption, previously men-

tioned, that the wild progenitor of maize was a lowland plant. Whatever may have been the nature of the original wild maize, it has given rise under domestication to varieties differing widely in their adaptation. Those introduced into Guatemala were apparently high-altitude varieties; at any rate only varieties adapted to high altitudes have survived the encroachment of the Tripsacoid types.

The importance of differences in altitude as natural barriers to promiscuous hybridization is emphasized by the situation in Huehuetenango. Here maize varieties with extremely low knob numbers, the lowest encountered in Guatemala, are found in Santa Eulalia while only eleven and fifteen miles away, at Jacaltenango and San Antonio Huista respectively, are found maize varieties with extremely high knob numbers. These localities though not far apart in distance are separated by more than 3000 feet in altitude. To one who has traveled in Guatemala and been transported from the steaming tropics near sea level to chilly mountain passes above the clouds in a distance of twenty-five miles by road, the effectiveness of this barrier is not difficult to appreciate, especially when it is associated, as it is in many cases in Guatemala, with actual physical barriers.

Size and shape of ear

No more than a casual inspection is required to show that in this collection, number of knobs is associated with size and shape of ears. Among the varieties with low-knob numbers are many ears with a pyramidal shape, the diameter at the butt larger than at the tip. Among varieties with high knob numbers the majority are almost cylindrical in shape. There is reason to expect such an association for in hybrids of maize and teosinte many of the segregates are more nearly cylindrical than the maize

parents, suggesting that *Tripsacum* germplasm produces effects in this direction. There is also reason to expect number of knobs to be associated with length of ear, for the C segment from teosinte increases the length of the ear in segregates from crosses of maize and teosinte. However, this occurs only when the C segment is acting alone. When other segments are present the ears are shorter.

No significant difference between low and high groups is shown in average length of ear on the basis of a four-fold table. There are some extremely long ears in the collection, however, and these are confined to varieties with intermediate knob numbers. None is found in the group with very low or very high knob numbers.

The groups do not differ significantly in diameter at base of ear and the difference in diameter at tip of ear is barely significant. There is a highly significant difference in the tip-base index which is derived by dividing diameter at tip by diameter at base. This tendency for the low-knob group to have tapering ears is shown still more strikingly in the taper index which expresses as a percentage the amount of reduction in diameter which occurs in each centimeter unit of length. Taper index is derived by dividing by length, the percentage difference between diameters at base and tip. The relationship between knob number and taper index is approximately linear.

Number and regularity of the rows

Another effect which *Tripsacum* germplasm produces in hybrids of maize and teosinte is a reduction in the number of rows of grain and a straightening of the rows. We might therefore expect both of these characters to be associated with knob numbers. The second expectation has been met but the first has not. The difference in the average number of rows in the low-knob and high-

knob groups is very small and is not significant. There is a highly significant difference, however, between knob numbers and regularity of rows. The population had originally been divided into three groups on the basis of this characteristic, the first in which the rows were so indistinct that their number was difficult to determine; the second in which the rows were irregular but still readily discernible; the third in which the rows were distinct and straight. For purposes of computation, the first two groups were combined. In spite of this loss of refinement there is a highly significant relationship with knob number. The Chi square computed from a fourfold table is 51.4, the highest value encountered in any of the relationships studied. It was probably this character, more than any other, which was unconsciously taken into consideration in classifying some of the ears as "Andean," for it is a fact that ears of the Andean region usually exhibit decidedly irregular rows of grain.

Firmness of the cob

Associated with a cylindrical ear and straight rows of grain is a hard, stiff cob holding the grains so firmly that they do not yield when pressure is applied with the thumb. In ears of many Andean varieties the kernels are easily pushed into the cob. Dr. Hugh C. Cutler who has travelled extensively in Guatemala tells us that the Indians are familiar with this characteristic and that in certain regions they discriminate against ears in which the kernels yield to pressure.

There is a relationship between this characteristic and knob number. When Chi square is computed from a fourfold table, the relationship does not appear to be significant, but when the ears are divided into three categories instead of two on the basis of firmness of the cob, a significant relationship can be shown.

It is not clear precisely what is represented by the firmness of the cob but it probably expresses at least two separate factors—the strength of the stalk to which the base of the caryopsis is attached and the rigidity of the glumes. The firmness of the cob is associated also with resistance to shattering. Ears of the Andean types usually shatter easily while some of the more Tripsacoid varieties and segregates from maize-teosinte crosses can be shelled only with difficulty. Tripsacum seems to impart to its derivatives a decided coriaceous quality which affects all parts of the cob and, indeed, practically all parts of the plant.

Size and shape of seeds

Tripsacum seeds are quite small and it would be expected that size of seed in maize would decrease with the amount of Tripsacum admixture. This has proved to be the case. Three measurements, number of seeds per row, number of seeds per unit (one cm.) of row and weight of ten seeds, all concerned with the size, and, to some extent, with the shape of the seed, show highly significant differences between the low and high groups. The greatest difference is shown in weight of seed which suggests that shape is a minor factor, as it is not involved in weight. There is little doubt, however, though it has not been demonstrated statistically, that differences in shape are also associated with knob number. We have not succeeded in devising any simple method of measuring the differences in shape though it is apparent that they exist. Among the low-knob group for example, are found ears of the Andean type in which the caryopses frequently approach a spherical shape and in which there is a considerable variation in size. These characteristics, combined with the irregularity in rows and the short tapering ear, make the entire structure comparable to a compact bunch of grapes. In the high-knob group, on the other

hand, the extreme type is one in which the grains are flat, uniform in size and shape and very regularly spaced in straight rows.

Endosperm type

It was suggested by Mangelsdorf and Reeves (18) that the pointed-seeded pop corns of Mexico and Central America are the most Tripsacoid types which have resulted from admixture with *Tripsacum* and that dent types originated from hybridization of these with uncontaminated flour corn. The Guatemalan varieties do not support this suggestion. Among the high-knob group, especially among varieties with ten knobs or more, dent corn is the predominating type. No pointed pop corns were included in McBryde's collection, although varieties with decidedly pointed seed occur. It is possible that the pointed-seed pop varieties are still to be collected in Guatemala but it is also possible that the original assumption that they are the most Tripsacoid types is in error. It is obvious now that such an assumption is not required inasmuch as *Tripsacum* and teosinte are themselves popping cereals (Beadle (4); Mangelsdorf and Reeves, unpublished), and there is no reason why a hybrid of teosinte and flour corn should not give rise directly to dent types. Such hybrids are now being investigated.

In the meantime it is clear that there is a relationship (P is less than .01) between knob number and dent types as opposed to typical flint or flour types. The two latter types are combined for purposes of computation. They differ from each other primarily by a single gene and there are several examples in our collection, of ears almost identical in all characteristics except that one is flinty, the other floury. Denting, on the other hand, is governed by a number of genes and is a complex departure from the basic flint and flour types.

Plant colors

There is no reason to expect a relationship between knob numbers and the various plant colors; all are encountered frequently in both Andean and Tripsacoid types of maize. No relationship was found between knob number and pericarp color, aleurone color or cob color, and the data are not included in Table II. Highly significant relationships were found, however, between knob number and endosperm color and knob number and purple plant color. Varieties with yellow endosperm predominate in the low-knob group, varieties with white endosperm in the high-knob group. What this means, if anything, in terms of *Tripsacum* contamination is difficult to see. It might suggest that the greater the amount of *Tripsacum* admixture the more likely is the *y* allele from *Tripsacum* to be included, but this suggestion does not appear especially plausible when alleles involved in other plant colors are not so affected. Indeed in the case of purple plant color, the gene for which presumably derives from maize, the relationship is reversed. Here the proportion of purple plants is significantly greater in the high-knob than in the low-knob group even when allowance is made for the low frequency in which purple plants appear. The reason for the relationship between these two plant colors and knob number is not clear.

Nature of the seminal root system

Seedlings of Andean type maize and of the infrequently knobbed Guarani maize of Paraguay are characterized by coarse, vigorous, primary and secondary seminal roots possessing a relatively small number of tertiary roots. Seedlings of *Tripsacum*, teosinte and strongly Tripsacoid maize have more fibrous root systems; the primary roots are slender and thread-like, the tertiary roots abundant. The two extreme types of root systems

may be conveniently designated as coarse and fibrous.

There is a highly significant relationship between knob number and the nature of the seminal root system. The relationship is closer than the data in Table II indicate, since varieties with intermediate knob numbers tend to have intermediate root systems, a fact which is not revealed when only two categories with respect to each characteristic are utilized.

Pubescence of sheaths

Many of the Guatemalan varieties exhibit highly pubescent leaf-sheaths and this characteristic is almost universal in the maize varieties of the central plateau of Mexico. We have encountered no South American varieties with knobless chromosomes in which this character occurs, and since at least one species of *Tripsacum*, *T. pilosum* Scribn. & Merr., is highly pubescent we might infer that this character, when it occurs in maize, has been derived from *Tripsacum*. Dr. Cutler, on the basis of his extensive observations and collections in Mexico and Guatemala, is of the opinion, however, that pubescence is a maize character and that at least part of the pubescence in *Tripsacum* is the result of the introgression of maize into *Tripsacum*. There is no doubt that some species of *Tripsacum* are heterozygous for pubescence. The senior author has found near Guadalajara, Mexico, pubescent and glabrous plants, apparently of the same species, growing in the same colony.

But, whatever may have been its origin in *Tripsacum*, pubescence, in Guatemalan maize, is undoubtedly a character derived from maize. The teosinte of San Antonio Huista is glabrous, and apparently the *Tripsacum* which grows in this area is also glabrous, for Kempton and Popenoe (9) describe it as "probably *T. laxum*," a species, which so far as we know, is always glabrous.

Furthermore there is a highly significant relationship between knob numbers and pubescence, pubescence being associated with low-knob numbers, smoothness with high numbers. The relationship is so strong and clear-cut that it allows us to make the prediction that knobless varieties of maize with pubescent leaf-sheaths will be discovered in South America when a thorough search is made.

Hairy sheath in maize has been reported as a simple Mendelian dominant by Tavcar (21). It may behave this way in certain cultures, when, for example, knobless pubescent stocks are crossed with knobless glabrous stocks. Among the Guatemalan varieties, however, its presence or absence is related to the number of knobs. All varieties with three knobs or less were strongly pubescent, all varieties with five knobs or less were pubescent to some degree. Among varieties with eight knobs or less only four in ninety-four were glabrous. In contrast, among varieties with twelve knobs or more only one in twenty-nine was pubescent and all varieties with thirteen knobs or more were glabrous. In this particular population a minimum of six knobs and usually eight or nine knobs are required to suppress pubescence, while the presence of twelve or more practically eliminates pubescence.

Pubescence, if it does not prove to be too widely distributed among South American varieties, may enable us to determine the region from which the Andean types of maize were introduced into Central America, for all of the Andean types so far discovered in this region are pubescent.

Smut infection

The planting at Forest Hills was made on a piece of land which had been heavily manured. As a consequence infection with smut, *Ustilago Zeae* (Beckm.) Ung., was extremely severe. The data in Table II show that there

is a highly significant negative relationship between knob number and percentage of plants infected with smut. Since *Tripsacum* has never been reported as a host for this organism and is apparently not susceptible to this disease, the relationship between knob number and resistance to smut is presumably due to the genes for resistance introduced from *Tripsacum* with the knobs.

Here, as in the case of altitude and pubescence, the low-knob group is comparatively uniform. All varieties with six knobs or less were infected by smut, every plant in some cases being severely infected. Varieties completely free of smut are encountered only among those with seven knobs or more. However, among varieties with as many as twelve knobs or more, are several which are strongly susceptible to smut; while Florida teosinte, with even more knobs than the most *Tripsacoid* maize, exhibits marked susceptibility under certain conditions. The relationship between knob number and smut resistance is obviously not a simple one.

Lodging

At both New Haven and Forest Hills many varieties were completely lodged. The stalks of some of these were so brittle that they snapped at the slightest tension; other varieties stood erect throughout the entire season despite a severe storm. These differences are strongly associated with knob number, the percentage of lodged plants decreasing progressively as the number of knobs increases. Here again, however, the low-knob group is reasonably uniform. Among varieties with six knobs or less only two had all of their plants erect at the end of the season, while about half of the varieties in this group had all plants prostrate and tangled.

Differences in lodging are associated with the internal structure of the stalk. Varieties with tender, brittle stalks

have practically no rind and the vascular bundles are widely scattered. At the other extreme are varieties with stalk so tough and strong that it is almost impossible to cut them with anything short of an ax. In these varieties the rind is prominent and the vascular bundles numerous, characters which are definitely Tripsacoid.

INTERRELATIONSHIPS OF CHARACTERS

Since practically all of the characteristics considered here have shown a relationship with knob number, it is to be expected that they should also show interrelationships among themselves. These relationships exist and can undoubtedly be demonstrated statistically in many cases. It is not within the scope of this paper to examine this problem in detail but it should be pointed out how frequently certain characteristics are associated in the low-knob group. All but two of the varieties with six knobs or less are grown only at high altitudes, 6500 feet or more. All of them are susceptible to smut; all except one have pubescent leaf-sheaths; all except two are susceptible to lodging; all but five have non-fibrous root systems. In the high-knob group, however, this association breaks down, although it does not disappear completely. Among varieties with seven knobs or more, are thirteen which lack pubescence but show fifty per cent or more of lodging; while four pubescent varieties show no lodging and five additional ones show only ten to twelve per cent. A similar situation obtains with respect to the pubescence-smut and lodging-smut relationship.

All of this indicates that the low-knob group is a fairly homogeneous one only slightly affected by such *Tripsacum* admixture as it has received. This in turn suggests that there is a threshold below which the *Tripsacum* admixture has very little effect, at least upon some characters. After this threshold is crossed, the effect is not

completely proportional to the number of knobs and this may suggest that the *kind* as well as the *amount* of *Tripsacum* germplasm is a factor in the results.

In any event the high-knob group is not a homogeneous one, and it represents a complex mixture of characters derived from pure maize on the one hand and from *Tripsacum* on the other. The task of recognizing and classifying its races will be a formidable one even with the useful diagnostic characters which Anderson and Cutler (2) have brought to bear upon the problem of racial differences in maize.

The relative homogeneity of the low-knob group as contrasted with the marked heterogeneity of the high-knob group is not in keeping with Longley's suggestions, discussed in greater detail later, that a high-knob number signifies primitiveness. For, regardless of whether the characters which we have considered are primitive or otherwise, it would seem to be a difficult evolutionary step to bring together in the low-knob or "advanced" group all of the characteristics which are scattered at random through the varieties of the high-knob or "primitive" group. Evolution seldom, if ever, operates in this direction.

INTERPRETATION AND CONCLUSIONS

How are we to interpret the various facts revealed by these studies of Guatemalan maize? 1. the great diversity in external morphological characters as well as in internal chromosome morphology; 2. the concentrated diversity occurring in one small area in Huehuetenango where teosinte is found in the wild and *Tripsacum* grows in profusion; 3. the relationship between knob numbers and other characteristics; 4. the restriction of low-knob varieties to high altitudes; and 5. the fact that practically all low-knob varieties are identical in certain char-

acteristics including pubescence, coarse seminal root systems and susceptibility to lodging and smut. A separate interpretation for each of these phenomena has already been suggested and we are now ready to draw the imaginary picture into which these more or less unrelated facts can be integrated.

At some time after maize had been domesticated in South America, a variety or a small group of varieties of cultivated maize was introduced into Central America. The ears of this maize were short and tapering, the cob was soft, the kernels fairly large but variable in size and very irregularly arranged upon the rachis. The plants exhibited pubescent leaf-sheaths and were decidedly susceptible to smut and lodging and this maize was satisfactory for culture only at high altitudes. We do not know whether the culture of this maize was ever widespread; at the present time it seems to be confined in Guatemala to the Departments of Quezaltenango, Totonicapan, El Quiche, Huehuetenango and probably San Marcos, and in Mexico to the State of Chiapas. We cannot determine whether it was grown at lower altitudes in this region but if it was it has now been completely replaced.

Some years or perhaps centuries after its introduction, in a small area in Huehuetenango, this South American maize hybridized with a species of *Tripsacum* by which some of the maize fields were surrounded. The first generation hybrid backcrossing once or repeatedly to its maize parent gave rise to a new plant, teosinte, in which the chromosome morphology closely resembled that of maize, except for certain pycnotic enlargements on the chromosomes imparted by the *Tripsacum* parent together with several simply inherited morphological characters⁵

⁵ Langham (11) has shown that in crosses of Durango teosinte and maize, two of the important characters which distinguish maize from both teosinte and *Tripsacum* (paired spikelets and polystichous pis-

of *Tripsacum* which enabled the new plant to survive in the wild.

As a result of this hybridization there also arose new varieties of maize with varying numbers of *Tripsacum* knobs. The knobs themselves, comprising only heterochromatin, had no genic effects, but associated with the knobs were usually small segments of *Tripsacum* chromatin homologous or partially homologous to those in maize. This admixture with *Tripsacum* chromatin produced profound modifications in the maize. New varieties came into existence in which the seeds were smaller, more inclined to be indented, more uniform in size and shape and arranged in straight rows on the rachis. The cobs became firmer and less susceptible to shattering, the stalks became tough and resistant to lodging, the leaf-sheaths became glabrous instead of pubescent and the plants became resistant to smut. These new *Tripsacoid* varieties were much superior to the pure maize at lower altitudes, and rapidly replaced it, if indeed it was ever extensively grown there. At high altitudes, however, at 6500 feet and more, the original maize succeeded in holding its own and became but slightly contaminated with *Tripsacum*. In the meantime derivatives of the *Tripsacum* contaminated maize spread to all parts of Central, North and South America where maize is grown, except to the Andean region of Peru, Bolivia and Ecuador where pure maize (some of it quite similar in characteristics to the type introduced into Central America) continued, as it has in Central America, to resist the encroachment of the new varieties.

This imaginary picture accounts for all of the essential

tillate inflorescences) are inherited as simple Mendelian characters. Unpublished studies by the senior author show the inheritance to be less simple than this when Florida teosinte rather than Durango is one of the parents, but even here the situation is probably not unduly complex.

facts, and so far as we can determine, is in keeping with the facts of genetics, cytology, morphology and anthropology. Two minor details are lacking; the picture does not show how widespread the culture of pure maize had become before the hybridization with *Tripsacum* and it does not fix the date at which this hybridization occurred. These are questions which may be answered when studies of maize from other Central American countries and Mexico have been completed, and when botanical and archaeological data have been more completely correlated.

ALTERNATIVE INTERPRETATIONS

So far we have discussed relationship between knob number and other characteristics only in terms of *Tripsacum* admixture as postulated by Mangelsdorf and Reeves. There are two other hypotheses on the origin of maize which may be considered, that of Montgomery (19) and Weatherwax (22) which has maize, teosinte and *Tripsacum* deriving independently from a remote common ancestor and that of Ascherson (3) which has maize deriving directly from teosinte. The limitations of both of these hypotheses in accounting for all of the facts have been discussed elsewhere (18). It should be pointed out, however, that the particular data presented in this paper can, without too much difficulty, be interpreted in terms of either of these alternative hypotheses, if other evidence bearing on the question is ignored.

Longley (15,16) has recently elaborated upon Ascherson's theory in interpreting the chromosome knob situation in the three American *Maydeae* and in drawing a picture of their possible relationship. A brief abstract of his conclusions follows:

The chromosomes of each species possess a definite and characteristic number of knob forming points. In *Tripsacum* and Guatemalan teosinte these points are more

numerous and are terminal; in maize and Mexican teosintes they are largely internal. The differences which now exist are assumed to be the result, not of structural changes, but of a few mutations which have affected chromosome gradients in such a way that knob positions in maize and Mexican teosintes are, on the average, closer to the centromere than in Guatemalan teosintes. Knob forming points, even though not visible, are regarded as always present. Knobs are formed only when adequate amounts of pycnotic material are available. Abundance of pycnotic material is associated with primitiveness. *Tripsacum* is regarded as the most primitive of the American Maydeae, standing near the base of the tree, teosinte from eastern Guatemala is regarded as the trunk of the tree; teosinte from western Guatemala as a major branch; maize and Mexican teosintes as the finer branches. It is suggested that maize originated directly from one of many teosinte strains. However, the suggestion, (Harshberger, 8; Collins, 5) that it has been derived from a hybrid of teosinte and an unknown grass, is not ruled out.

If we consider only the conclusion that an abundance of pycnotic material is associated with primitiveness, the relationship between knob numbers and other characteristics agrees almost as well with Longley's hypothesis as with that of Mangelsdorf and Reeves. In either case relationships between knob numbers and other characteristics are to be expected. The chief difference is that in one case the association is with "primitive" characteristics, in the other with "Tripsacoid" characteristics. The terms are partially synonymous but not completely so. Longley's hypothesis falls short in so many additional respects, however, that an interpretation of our data in terms of his hypothesis is virtually precluded.

Longley's conclusions are based almost wholly upon

chromosome morphology. This is certainly one of the most important types of evidence in a problem of this nature. However, it is not the only evidence available and it may be hazardous to overlook other types of data which can be brought to bear upon the problem. Furthermore the evidence from chromosome morphology does not support adequately the conclusions which have been drawn.

The presence of latent knob-forming points, invisible to the observer because adequate knob material is lacking, is questionable. If, when abundant knob material is supplied through hybridization, the knob-forming points still remain invisible, then another assumption—that the points have become temporarily inactive through disuse—is required (Longley, 16).

There is some question, too, whether the gradients affecting knob position actually exist. There is no necessity for assuming a gradient in teosintes with terminal knobs; if there is a gradient for terminal knobs there may well be a similar one for chromosome ends and telomeres. The internal knobs of maize certainly follow a rough pattern, at least they are not distributed at random over the chromosomes. No knobs are found in the immediate vicinity of centromeres. Perhaps there is some significance in the fact that they are most frequent in the general region where, if Darlington's (6) figures of chiasmata in maize are a criterion, crossing-over should be at a maximum. In any case the actual distribution of the knobs shows a poor agreement with the theoretical gradient (Longley, 14). A better fitting gradient could, no doubt, be calculated but perhaps the knob positions do not conform to any gradient in the sense in which the term has been used.

Still greater difficulties are encountered, however, when one attempts to carry to a logical conclusion, in terms of

known genetic and cytological mechanisms, the assumption that the knob positions in maize have been derived from those in teosinte, not by structural changes in the chromosomes, but as the result of a few mutations affecting the gradient. There is no doubt that chromosome behavior is partially gene-controlled. There are at least five genes in maize: asynaptic, sticky, polymitotic, and variable-sterile (two genes) affecting chromosome behavior and cell division (cf. Rhoades & McClintock, 20). In *Allium* there is a situation with respect to chiasmata which is almost identical with that of maize and teosinte with respect to knobs. In *A. fistulosum* the chiasmata are interstitially localized; in *A. cepa* the chiasmata are all terminal. The difference is due to a single recessive gene (Emsweller, 7; Levan, 12). But in this case as well as in similar cases all chromosomes in a single nucleus follow the same pattern; all are controlled by the same nuclear mechanism. In the F₁ hybrid of *A. fistulosum* × *A. cepa* all chiasmata are terminal. If the knob gradients in maize and teosinte are analagous, one must expect a decided shift in knob positions in F₁ hybrids of maize and teosinte. The internal maize knobs should move to the chromosome ends, most of the teosinte knobs should move to internal positions or both should move to intervening regions depending upon whether the mutant maize-gradient-controlling genes are recessive, dominant or intermediate in their effects. Such wholesale shifts have not been reported. In fact one has but to examine Longley's (13) illustration of the chromosomes in the F₁ hybrid of maize and Florida teosinte to be convinced that they do not occur.

Additional assumptions can be made, assumptions involving large numbers of mutant genes and the differential control of maize-gradient and teosinte-gradient chromosomes within the same nucleus. Longley (15)

apparently makes assumptions of this type when he interprets the knob situation in teosinte from western Guatemala. Here the four shortest chromosomes are supposedly controlled by the maize gradient, the six largest ones by the teosinte gradient, and the condition is regarded as one step in the evolution of teosinte to maize.

But all assumptions of this kind lead finally to the same impasse: recombinations resulting from segregation and crossing-over and involving the knobs of one species and the gradient-controlling genes of the other are inevitable. Hybridization of the two species is certain to be followed by general shifts in knob positions. Until such a phenomenon has been shown to occur, the basic tenet of Longley's hypothesis, that maize has stemmed directly from teosinte, will continue to remain inadequate in accounting for the established facts; as it has for more than fifty years since it was first proposed by Ascherson.

ANTHROPOLOGICAL IMPLICATIONS

There is no doubt that western Guatemala is a concentrated center of diversity of maize. In so far as diversity is associated with centers of origin and, in the absence of conflicting evidence, this region must also be regarded as *a* center if not *the* center of origin for cultivated maize varieties.

If the older hypotheses which have maize deriving directly from teosinte are accepted, the implications are clear. In that case the region comprising the Department of Huehuetenango and perhaps the adjoining Departments of El Quiche, Totonicapan, Quezaltenango and San Marcos (as well as the adjoining State of Chiapas in Mexico) is the *primary* and probably the *only* center of domestication of maize. Presumably it is also the center where maize agriculture originated and from which it spread to all those parts of the New World where it was

practised in pre-Columbian times. In spite of numerous facts which are not in harmony with such a conclusion, the only evidence shown by Guatemalan maize varieties which is seriously in conflict, is the complete absence of varieties exhibiting any of those successive morphological changes which must have occurred in the evolution of a wild teosinte to a cultivated maize. Only the initial raw material and the end-product are now in evidence. All of the intermediate steps which must have occurred have been completely and miraculously erased, and this has happened in a region where very distinct varieties of maize have maintained themselves in a relative state of purity in localities not more than a few miles apart.

If, however, the newer hypothesis,—that teosinte is the hybrid progeny of maize rather than its progenitor,—is accepted, then this region is a secondary rather than the primary center of origin of cultivated maize varieties. It is not the area where maize culture originated or the focus from which it spread to all parts of the Americas. It is, however, the center from which the majority of maize varieties now cultivated in Central America, North America, the lowlands of South America and the West Indies, have been derived. This hypothesis requires the assumption that maize was introduced into Central America from South America. The fact that varieties are found in Guatemala which resemble those of the Andean region, not only in external appearance but also in their internal chromosome structure, appears to satisfy this assumption. This does not mean, however, that the area in western Guatemala where the hybridization with *Tripsacum* occurred is also the area into which maize was first introduced from South America. There may have been a widespread culture of Andean types of maize in Central America and even in parts of North America before the hybridization with *Tripsacum* occurred.

In so far as the history of maize has any bearing upon the problems of the pre-Columbian American cultures, it is evident that the anthropologist is faced with two clear-cut alternatives. Either the region in western Guatemala is the center of origin of all maize, of maize agriculture and the prehistoric cultures based upon maize agriculture; or it is no more than a secondary center from which maize varieties, originally introduced from South America and subsequently modified by admixture with *Trip-sacum*, have spread.

Many anthropologists may continue to prefer the first alternative but some have seen the possibilities in the second. Both Kidder (10) and Lowie (17), in discussing the complete lack of evidence on cultures antecedent to the already well-developed "Archaic" in Middle America, have pointed to the inadequacy (from the anthropological standpoint) of the commonly accepted view that maize is derived from teosinte. Kidder's statements in this connection are of particular interest, because his suggestions (made before the hypothesis of Mangelsdorf and Reeves was published) anticipate several of their conclusions, as is demonstrated by the excerpts which follow:

"In the above guesses as to the time and location of basic New World culture first consideration has been given to the Middle American highlands: because agriculture seems to be a prerequisite necessity for the development of such a culture; because maize was the New World staple; and because *teocentli* currently believed to have played a part in the origin of maize, is apparently only to be found in those regions. . . .

The supposed rôle of Middle American *teocentli* in the ancestry of maize may, however, have confused us. Other possibilities must be considered, *Teocentli* may not have fathered maize; it may yet be found in South America. Some other plant ancestor, as yet undiscovered, perhaps even extinct as result of maize culture in the lands favorable to its growth, may exist or have existed in South America. . . .

If maize should prove to derive from South America the whole setup would in some respects be more comprehensible."

SIGNIFICANCE IN MAIZE BREEDING

As the plant breeder begins to reach a point of diminishing returns in improving the varieties at hand, he is compelled to turn to centers of diversity for new characters. The maize varieties of western Guatemala, especially the Tripsacoid types, those with high knob numbers, constitute an untapped reservoir of germplasm which includes genes governing the expression of a number of valuable characteristics including fibrous root systems, resistance to lodging, resistance to smut and perhaps to other diseases. Here in concentrated form is to be found much of the germplasm which occurs greatly diluted in the commercial varieties of the United States.

There are few, if any, varieties in western Guatemala which would, as such, be useful for commercial production in the United States. Perhaps a few would have a place as silage corn, but even this is doubtful; the stalks are too tough to be cut with ordinary machinery. But if the breeder is looking, not for varieties but for genes, he will certainly find in Guatemalan maize, many which may be useful.

Most of the Guatemalan varieties are characterized by extreme lateness in maturity. Whether this characteristic is readily separable from others, can be determined only by experiment. Unpublished observations by the senior author indicate that large differences in time of maturity of corn varieties may be governed by a relatively small number of genes. In crosses of the early maturing inbred strain P 39 with tall, late varieties of Texas, it was possible in the backcross to P 39 to recover the type of ear and productiveness of P 39 with much of the lateness and vigor of the Texas varieties. Also Brunson (unpublished) has found that the indeterminate growth habit of Cuzcoid (a type resembling in its vegetative habit the Cuzco variety of Peru) is a simple Mendelian recessive,

and Langham has found a similar situation in Durango teosinte. These facts suggest that the separation of useful from undesirable genes in Guatemalan corn may not be too difficult. In any case the possibility of utilizing in practical corn improvement this complex reservoir of potentially valuable germplasm is not one to be completely overlooked or indefinitely postponed since Latin America is facing the same danger which the Corn-Belt has already met,—the extinction of potentially useful varieties as the result of widespread planting of a few selected types.

SUMMARY

1. Chromosome knob counts, in 162 varieties from thirty-eight localities in western Guatemala, showed a range in knob numbers from one to sixteen.

2. All of the eighteen knob positions known in maize and in addition three positions not previously reported were encountered.

3. The greatest diversity was found in a small area in the Department of Huehuetenango where low-knob and high-knob varieties occur in close proximity. This is also the area in which teosinte is found growing in the wild.

4. The maize of western Guatemala exhibits great diversity in external morphological characteristics, but plants with six knobs or less are uniform in having pubescent leaf-sheaths, a coarse seminal root system and in susceptibility to lodging and smut. These varieties are found only at altitudes of 6500 feet or more.

5. The number of chromosome knobs is associated with various characteristics which may have been derived from *Tripsacum*.

6. The combined evidence suggests that a South American variety of maize—characterized by pubescent

leaf-sheaths, coarse seminal roots and susceptibility to lodging and smut—hybridized with a species of *Tripsacum* to produce the new genus *Euchlaena* and new varieties of maize exhibiting *Tripsacum* admixture.

7. Western Guatemala is thus regarded as a secondary center of origin of cultivated maize varieties.

8. The potential value for purposes of plant breeding of the *Tripsacoid* varieties of maize of Guatemala is pointed out.

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